The effect of quadriceps muscle fatigue on position matching at the knee

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This is a report of the effects of exercise on position matching at the knee. Young adult subjects were required to step down a set of stairs (792 steps), representing eccentric-biased exercise of the quadriceps muscle, or step up them, concentric-biased exercise. Immediately after eccentric exercise subjects showed a mean force drop of 28% (± 6%, S.E.M.) of the control value in their exercised quadriceps muscle, which was accompanied by 4.8 deg (± 0.8 deg) of error between reference and matching legs in a position matching task at the knee. Similarly concentric exercise was followed by a force drop of 15% (± 3%) and matching errors of 3.7 deg (± 0.4 deg). These effects were significant. The direction of the errors suggested that subjects perceived their exercised muscles to be longer that they actually were. This finding was not consistent with the hypothesis that the increase in effort required to support the leg after fatigue from exercise was responsible for the errors. It is hypothesized that position sense in an unsupported leg arises, in part, from operation of an internal forward model. When the motor command is increased to compensate for the effects of fatigue, the comparison between predicted and actual feedback from quadriceps leads to the impression that the muscle is longer than it actually is. The exercise effects on proprioception may have implications for sports injuries and for evaluation of the factors leading to falls in the elderly.

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This report is concerned with proprioception at the knee. The term 'proprioception' was introduced by. Sherrington (1906) to refer to 'sensations arising in special end organs which were adapted for excitation by changes going forward in the organism itself'. Within the range of sensations included under proprioception is the sense of position and movement of our body parts, called 'kinaesthesis' by Bastian (1880). Here we report observations on position sense at the knee.

In recent years a number of studies have reported that the kinaesthetic sense can be disturbed by exercise (Saxton *et al.* 1995; Brockett *et al.* 1997) including at the knee (Skinner *et al.* 1986; Lattanzio *et al.* 1997). More recently, disturbance to limb position sense has been described following both eccentric exercise, where the contracting muscle is lengthened, and concentric exercise, where it shortens (Walsh *et al.* 2004, 2006; Allen *et al.* 2007). Eccentric exercise is known to lead to muscle damage (Proske & Morgan, 2001), which raises the possibility that the damage is responsible for the disturbed sensation. However since similar effects were observed with concentric exercise, which is known not to be associated with significant damage (Newham *et al.* 1983*a*,*b*), this is unlikely.

Up to now most of our work has been done on position matching at the elbow joint. Specifically, we studied position matching after exercising elbow flexor muscles (Walsh *et al.* 2004; Allen & Proske, 2006; Allen *et al.* 2007). Here we have extended our studies to position matching at the knee before and after eccentric-biased or concentric-biased exercise of the knee extensor, quadriceps. Is this simply repeating the earlier observations on just another muscle group? Obviously proprioception in leg muscles is important both from the point of view of postural stability and for locomotion. However there is another reason why we chose to measure position matching ability at the knee.

In a position matching task at the elbow joint, the experiment is traditionally done by asking subjects to match the position of one arm by placement of the other (Goodwin *et al.* 1972). The experiment is done in the vertical plane and the subject supports their arms themselves. After exercise of one arm, matching errors with the other, unexercised arm lay significantly in the direction of extension (Walsh *et al.* 2004, 2006). Since similar errors appeared to be generated when the arm supported weights rather than being exercised (Winter *et al.* 2005), it suggested that the effort required to

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support the arm against the force of gravity provided the subject with information about its position. Following fatigue from exercise, the effort would be greater, leading the subject to believe that the arm was more extended, in a position where the gravitational vector was greater (Walsh *et al.* 2004).

However more recent studies by our group of position matching ability in the horizontal plane, where maintenance of limb position is largely independent of gravity, have not supported these ideas (Ansems *et al.* 2006; Allen *et al.* 2007). The experiments described here were designed to test two competing hypotheses. If effort played a role in position matching, the limb supported by the fatigued muscle would always be perceived as being more extended than it actually was, the subject believing that the extra effort was the result of supporting the limb in a position where the gravity vector was larger. A more extended forearm means a longer elbow flexor muscle, whereas a more extended leg means a shorter knee extensor. So the effort hypothesis predicts opposing effects of exercise on perceived muscle length at the elbow joint and at the knee. In the competing hypothesis we propose that a fatigued muscle is always perceived as longer than it is, leading, at the knee, to errors in a direction exactly opposite to that predicted by the effort hypothesis. The observations reported here supported the second of these hypotheses.

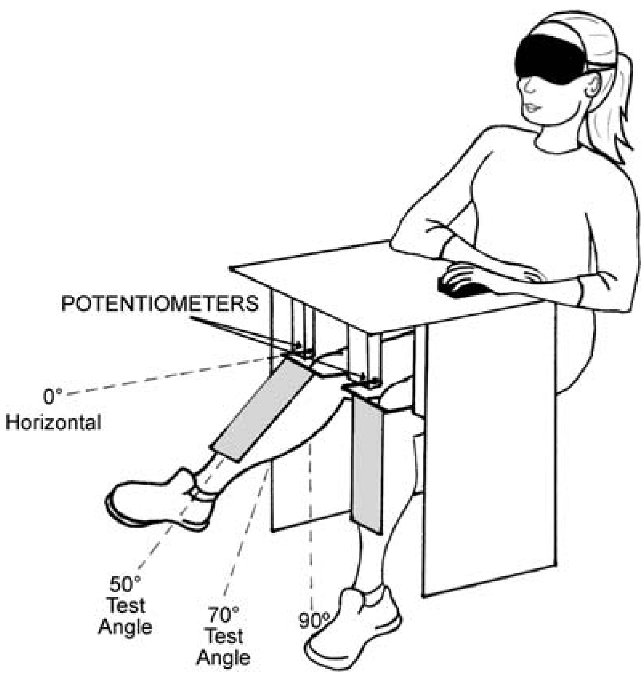

Figure 1. The experimental set-up
Blindfolded subjects sat in an adjustable chair mounted on a steel frame. Subjects' chair position and the apparatus height were adjusted by making sure the lateral and medial epicondyles of the knee were in line with the pivot point of the position matching apparatus. Both legs were strapped to a pair of lightweight paddles connected to potentiometers, whose voltage output was proportional to knee angle. The upper legs were held in position by knee clamps. A fully extended leg (horizontal) was assigned a value of 0 deg, and measurement of knee angle was given as degrees below the horizontal.

Methods

A total of 18 healthy subjects (4 males and 14 females) participated in the study. In the experiment on eccentric exercise eight subjects participated, two males and six females (20.2 ± 1.0 years). The concentrically exercised group included 10 subjects, two males and eight females; (20.0 ± 1.8 years). No subject carried out both forms of exercise.

Subjects with lower limb injuries or who had a previous history of cardiovascular or exercise-induced injury were excluded from the study. All subjects gave their written informed consent prior to participating in the experiments, which were approved by the Monash University Committee for Human Experimentation, and conformed with the ethical aspects of the *Declaration of Helsinki*.

Each subject was required to attend a familiarization session in which a series of control position sense measurement was carried out. Subjects were asked to participate further only if they achieved acceptable levels of reliability in their matching performance, which was set at a standard deviation of matching errors of less than 5 deg. All 18 subjects tested were able to achieve this level of matching accuracy.

Position matching task

Subjects were seated in an adjustable chair mounted on a steel frame. Subjects' chair position and the apparatus height were adjusted by making sure the lateral and medial epicondyles of the knee were in line with the pivot point of the position matching apparatus. The apparatus (Fig. 1), consisted of a pair of lightweight paddles connected to potentiometers, whose voltage output was proportional to knee angle. Subjects had each leg loosely strapped to the paddles. The upper legs were held in position by knee clamps, positioned just above the patella and fitted once the subject was correctly seated. The initial test position for each subject was recorded and maintained throughout the experiment. Knee angle was given as degrees below the horizontal which was assigned a value of 0 deg (Fig. 1). Position signals were acquired at 40 Hz using MacLab running Chart software (ADInstruments, Castle Hill, NSW, Australia) on a Macintosh computer.

For the position matching task, both legs were conditioned at 110 deg. For this, the experimenter asked the subject to contract the quadriceps muscles (push the leg out) at approximately 20% of their maximal voluntary contraction (MVC), while the experimenter held the leg in position at the conditioning angle (110 deg). The subject was then asked to relax, while the experimenter moved one leg (reference) to one of two test angles (50 deg or 70 deg from horizontal). The blindfolded subject was asked to maintain the position of the reference leg while they moved their other leg (indicator) to make a match. Subjects indicated that they had achieved a satisfactory match by pressing a switch. A single matching trial took approximately 20 s to complete. It was followed by a 2 min rest period before the next match was commenced. A total of 10 matching trials was carried out, with each of the two test angles being presented five times in a randomly assigned order. After a short rest period, the protocol was repeated, but this time with the roles of reference and indicator legs reversed, so that each leg was used as the reference for half of the trials. Position matching errors were calculated as the angular difference between the reference and the indicator leg. The same procedure was used for all three testing periods: pre-exercise, immediately post-exercise and 24 h post-exercise. Errors were assigned as positive when the indicator leg matched in the direction of extension relative to the reference leg and as negative when the indicator leg matched in the direction of flexion.

Maximum voluntary contraction (MVC)

Subjects were seated in the chair of a dynamometer (Kin-Com Chattanooga Group Inc., Chattanooga, TN, USA). The seat position was adjusted so that the pivot point of the dynamometer head was in line with the lateral epicondyle of the knee. The leg brace was strapped to the lower leg at 60% of the lower leg length, measured as the distance from the lateral epicondyle to the lateral malleolus.

Once correctly positioned, subjects' hips and trunk were strapped to the dynamometer chair by means of seat belts to isolate the leg and prevent upper body movement during the knee extensions.

Subjects were asked to generate a total of three consecutive MVCs with a randomly assigned leg, followed by three consecutive MVCs with the other leg. They were required to push as hard as they could (extending the knee) against the leg brace for 3 s at the knee angle of 70 deg, the approximate optimum angle for quadriceps (Newman *et al.* 2003; Bowers *et al.* 2004), followed by a rest period. Visual feedback of torque output, as well as verbal encouragement by the experimenter were provided during each trial. Torque signals were acquired at 40 Hz using MacLab running Chart software (ADInstruments) on an IBM computer. The maximum torque for each leg was calculated from the highest value reached during one of the three MVCs. These measurements were taken pre-exercise, immediately post-exercise (0 h) and at 24 h post-exercise.

The exercise

For each subject the quadriceps muscle of one leg was subjected to a period of exercise. The leg to be exercised was chosen as the subjects' dominant leg. Subjects found it easier to carry out the exercise in this way.

Eccentric exercise

For this exercise the non-dominant leg was always chosen as the lead leg with which to step down the stairs. Both legs started on the same step and then the lead leg stepped down two steps at a time while the other leg supported the weight of the body. This led to some flexing of the supporting leg, thereby lengthening quadriceps, while it was contracting and representing an eccentric contraction.

Subjects walked down six flights of stairs, two steps at a time, until they had completed 11 circuits representing a total of 792 steps. Subjects were transported to the top of the stairs by an elevator. One circuit took 5 min to complete. The subjects' speed was monitored with a stopwatch, and they were regularly given feedback about the time left for completion of the circuit. This helped subjects maintain a constant speed. Of the eight subjects, four performed the exercise task carrying a rucksack containing weights representing 10% of their total body weight. These subjects had a history of exercise and sporting activities in daily life and the extra load was used to ensure that the exercise was sufficient to produce significant fatigue.

Concentric exercise

The concentric exercise required subjects to climb up a set of stairs. Both legs started on the same step. The lead (dominant) leg stepped up two steps at a time, and the subjects then shifted their weight to this leg, extending it while moving up the stairs, and bringing the other, largely passive leg with it. This process of transfer of body weight up the stairs was performed predominantly by knee extension, involving contraction and shortening of the quadriceps muscle.

Subjects walked up six flights of stairs, two steps at a time, until they had completed this 11 times, representing 792 steps. Each time the subjects reached the top of the stairs, they were transported via an elevator back to ground level to repeat the exercise. The time taken to complete one circuit was also kept at 5 min. All subjects carried a rucksack with a load representing 10% of their total body weight. This increased the intensity of the exercise to achieve sufficient levels of fatigue.

Muscle damage indicators

At each of the three time points (pre-exercise, immediately post-exercise and 24 h post-exercise) a measurement of muscle soreness was made. The level of soreness was taken as an indicator of the amount of muscle damage present following the exercise. Subjects were asked to lower their bodies into a squatting position while they rested their back against a wall. This stretched quadriceps and generated soreness. The mean value of three successive measurements was reported. Subjects were asked to subjectively rate their level of muscle soreness on a visual analog scale (VAS) of 0–10, with 0 representing 'no soreness' and 10 the 'worst possible soreness'. A diagram of a human body was also presented so that subjects could indicate the specific area(s) of soreness.

Statistics

Data was analysed using Igor Pro version 4 (Wavemetrics, Lake Oswego, OR, USA) software running on a Macintosh computer. SPSS (SPSS Inc., Chicago, IL, USA) was used for statistical analysis. A repeated measures ANOVA was used to test matching errors over the three time points (pre-exercise, immediately post-exercise, 24 h post-exercise), when the exercise leg acted as the reference and when it acted as the indicator. A repeated measures ANOVA was also used to test the force over the three time points for both the exercised leg and control leg. The soreness rating pre-exercise, immediately post-exercise, and 24 h post-exercise was analysed using a repeated measures ANOVA. Where significance was found, Tukey's *post hoc* test was used for individual comparisons. For all tests, $P < 0.05$ was accepted as statistically significant. Values for pooled errors from different subjects are given as means ± standard error of the mean (S.E.M.).

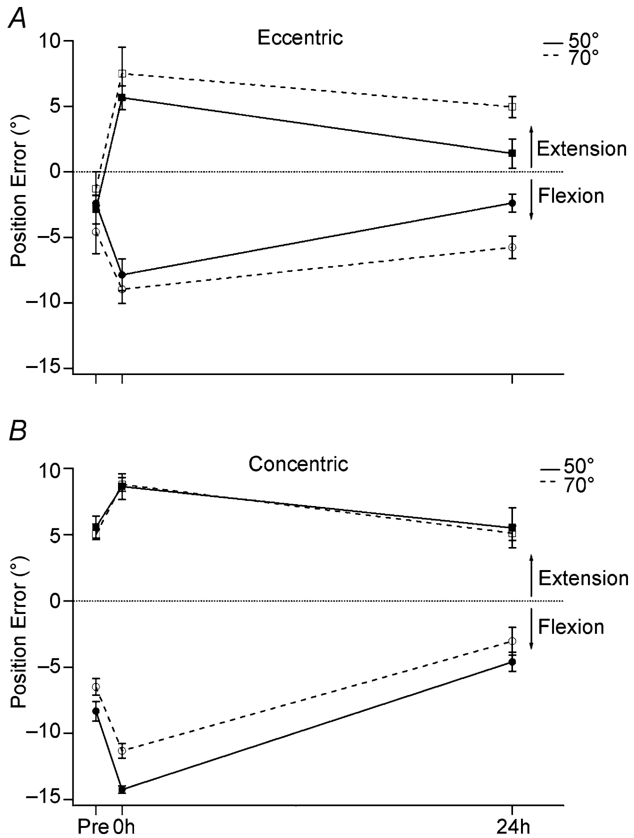

Figure 2. Position matching errors for a single subject
A, errors before (Pre), immediately after (0 h) and 24 h (24 h) after a period of eccentrically biased exercise of knee extensors. Filled symbols and continuous line, test angle 50 deg. Open symbols and dashed line, test angle 70 deg. Circles, when the exercised leg acted as the reference; squares, when the exercise leg acted as the indicator. Errors are shown as the angular difference in position between reference and indicator legs. When the position of the indicator leg lay in the direction of leg extension, errors were scored as positive, and when they were in the direction of flexion they were negative. Dotted line, zero error. All values are means (± S.E.M.) of 10 trials. *B*, position matching errors at the knee for another subject before and after a period of concentrically biased exercise of knee extensors. Symbols as in *A*, with all values means (± S.E.M.) of 10 trials.

Results

Eccentric exercise

All eight subjects successfully completed the exercise. Each subject had developed significant soreness in their exercised quadriceps by 24 h post-exercise.

Fall in force

Subjects showed a significant fall in force to 69.8 ± 4.8% of the pre-exercise value in the exercised quadriceps immediately after the exercise (Fig. 3). By 24 h post-exercise there was some recovery to 76.2 ± 4.1%. Analysis revealed a significant difference in force over the three testing sessions ($F_{2,14} = 10.98$, $P < 0.05$). By comparison, the fall in force for the control leg was to 98.4 ± 4.9% immediately after the exercise, which had recovered to 103.0 ± 2.9% at 24 h. For the control leg there was no significant difference in values for force over the three testing sessions.

Muscle soreness

Apart from the sustained fall in force after the eccentric exercise, the other indicator of muscle damage used in this study was muscle soreness. Mean soreness pre-exercise, on a VAS of 0–10 was 0.4 ± 0.2. In the exercised muscle this increased to 1.9 ± 0.3 immediately after the exercise and 3.1 ± 0.4 at 24 h. Soreness was significant over the three testing sessions ($F_{2,7} = 18.11$, $P < 0.05$). On all occasions soreness was restricted to the knee extensors of the exercised leg.

Position matching

Errors in position matching accuracy for one subject before and after a period of eccentric exercise are shown in Fig. 2. This subject had a force drop in the exercised leg to 77.5% of the pre-exercise value immediately after the exercise.

When the exercised leg acted as the reference, mean matching errors before the exercise were -2.4 ± 0.6 deg at a 50 deg test angle and -4.6 ± 1.7 deg at a 70 deg test angle. Immediately after the exercise the subject matched the reference position by placing the indicator leg further in the direction of flexion. The matching error was -7.9 ± 1.2 deg at 50 deg test angle and -9.0 ± 1.1 deg at 70 deg test angle. At 24 h post-exercise, errors had become smaller with values of -2.4 ± 0.7 deg at 50 deg and -5.8 ± 0.9 deg at 70 deg.

When the exercised leg acted as the indicator, the subject matched the position of the reference leg by adopting a more extended position with the indicator leg. Pre-exercise errors were -2.9 ± 1.1 deg at 50 deg test angle and -1.3 ± 1.3 deg at 70 deg test angle. Immediately post-exercise, the matching error was $+5.7 \pm 0.9$ deg at 50 deg and $+7.5 \pm 2.0$ deg at 70 deg. Errors had reduced by 24 h to $+1.4 \pm 1.1$ deg at 50 deg and $+5.0 \pm 0.8$ deg at 70 deg. Since differences in position errors for the two test angles were small and not significant, these data were combined. The pooled distribution for the eight subjects using the combined data is shown in Fig. 3. When the exercised leg acted as the reference, pre-exercise errors were 0.2 ± 1.2 deg. Immediately after the exercise mean matching error was -4.5 ± 1.6 deg and this fell by 24 h to a mean of -1.6 ± 1.3 deg. A repeated measures ANOVA showed that there were significant differences in the distributions of the errors at the three measurement times ($F_{2,14} = 7.42$, $P < 0.05$). *Post hoc* tests revealed that there was a significant difference in the errors before compared with immediately after the exercise.

When the exercised leg acted as the indicator, pre-exercise errors were $+1.6 \pm 1.4$ deg. Immediately after the exercise mean errors were $+6.5 \pm 1.8$ deg. They fell to $+5.3 \pm 2.1$ deg at 24 h. Analysis showed that these changes were significant ($F_{2,14} = 9.54$, $P < 0.05$). *Post hoc* tests showed that values both immediately after the exercise and at 24 h were significantly different from the pre-exercise value.

Concentric exercise

Of the 10 subjects who embarked on this study, 8 completed it successfully. Two subjects were excluded, one because the fall in MVC was only 5%, the other because the subject developed some soreness in their control leg during the course of the exercise.

Fall in force

Changes in force for both the exercised and unexercised muscles for the eight subjects are shown in Fig. 4. After the exercise, the exercised muscle showed an immediate fall in force to $85.5 \pm 2.7\%$. By 24 h post-exercise, force had recovered substantially and was back to $98.2 \pm 2.7\%$ of the pre-exercise value. There was a significant difference in force for the exercised leg over the three measurement periods ($F_{2,14} = 10.78$, $P < 0.05$). *Post hoc* tests revealed that the fall in force immediately after the exercise was significant, as was the degree of recovery by 24 h. The control leg showed a fall in force to $94.1 \pm 2.7\%$ immediately after the exercise, but this had fully recovered by 24 h. There was no significant change in force over the three testing sessions.

Muscle soreness

None of the subjects who carried out the concentric exercise reported any delayed onset muscle soreness.

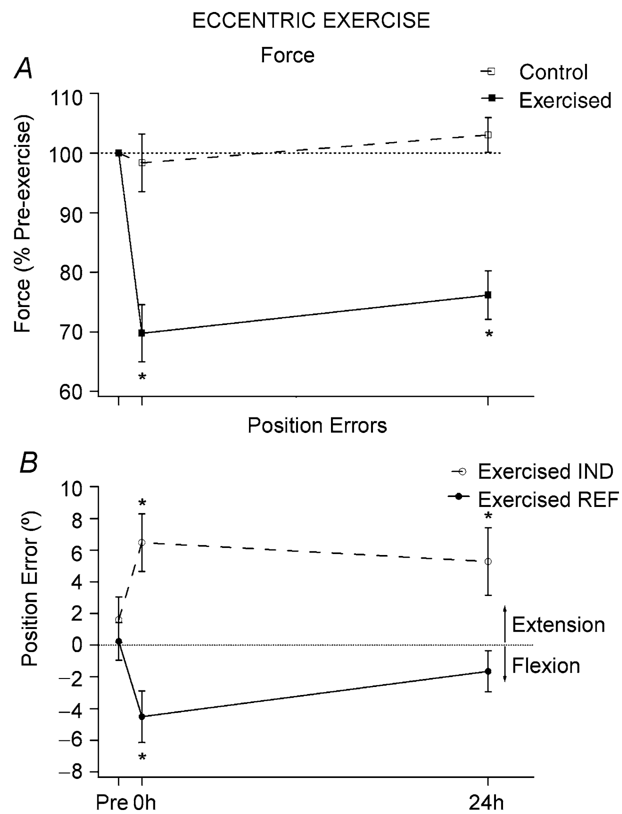

Figure 3. Pooled data from eight subjects after eccentric exercise

A, changes in knee extensor MVC after exercise. The pre-exercise value (Pre) has been assigned 100%. Force remaining immediately after the exercise (0 h) and at 24 h (24 h) has been compared for the exercised leg (filled symbols, continuous line) and the unexercised leg (open symbols, dashed line). Dotted line, 100%. Asterisks indicate significant differences from pre-exercise values. *B*, position sense errors at the knee. Filled symbols, continuous line, errors measured when the exercised leg acted as the reference. Open symbols, dashed line, the exercised leg acted as the indicator. Dotted line, zero error. Errors in the direction of extension have been scored as positive, in the direction of flexion as negative. All values are means (± S.E.M.). Asterisks indicate significant differences from pre-exercise errors.

Position matching

Position matching accuracy was measured for 50 deg and 70 deg test angles, pre-exercise, post-exercise and at 24 h. The data for a single subject are shown in Fig. 2. Pre-exercise values for 70 deg were $+5.0 \pm 0.4$ deg. Immediately after the exercise this increased to $+8.8 \pm 0.5$ deg. At 24 h errors had fallen to $+5.1 \pm 0.5$ deg. For the 50 deg test angle, pre-exercise values were $+5.6 \pm 0.8$ deg, which increased to $+8.6 \pm 1.0$ deg immediately after the exercise and then fell to $+5.5 \pm 1.5$ deg at 24 h. When the exercised leg acted as the reference, errors lay in the opposite direction. For the 70 deg test angle, the pre-exercise value was -6.5 ± 0.6 deg. This fell further to -11.3 ± 0.5 deg after the exercise. At 24 h errors had reduced to -3.0 ± 1.1 deg. For a 50 deg test angle, pre-exercise values were -8.3 ± 0.7 deg. After the exercise this had increased to -14.2 ± 0.3 deg and it reduced to -4.6 ± 0.7 deg at 24 h.

Since subjects showed no significant differences in errors for the two test angles (Fig. 2) their values were combined. The pooled data for the eight subjects are shown in Fig. 4. When the exercised leg acted as the reference, pre-exercise errors were 0.3 ± 1.1 deg. After the exercise errors increased to -2.7 ± 1.4 deg and then reduced at 24 h to -0.4 ± 1.0 deg. A repeated measures ANOVA showed that there was a significant difference in the errors between testing sessions ($F_{2,14} = 10.09$, $P < 0.05$). *Post hoc* tests revealed that the errors immediately after the exercise were significantly different from control values.

When the exercised leg acted as the indicator, errors lay in the direction of extension. Pre-exercise errors were $+2.0 \pm 1.9$ deg. After the exercise these increased to 4.1 ± 1.5 deg. By 24 h after the exercise errors had fallen to $+2.1 \pm 1.1$ deg. A repeated measures ANOVA revealed a borderline significant difference between testing sessions ($F_{2,14} = 3.43$, $P = 0.06$).

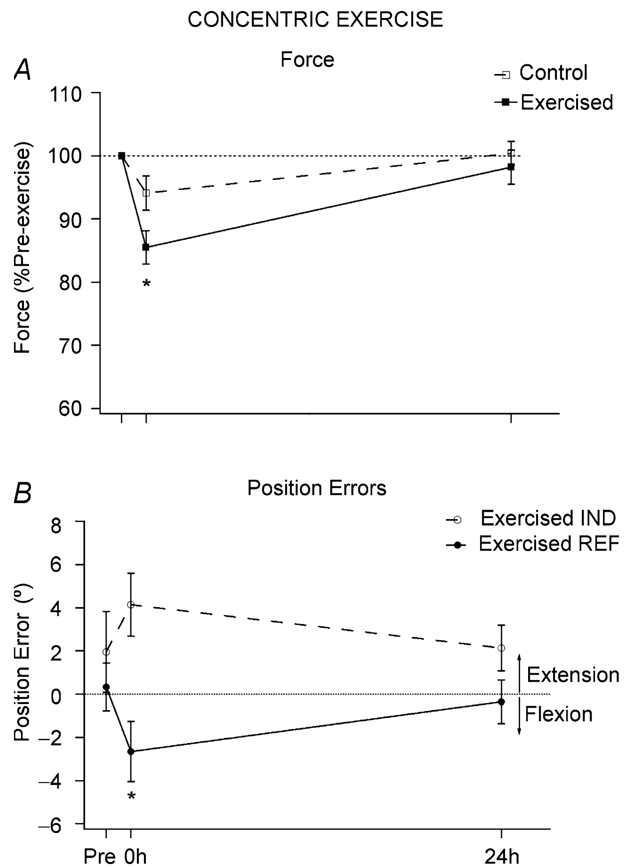

Figure 4. Pooled data for eight subjects after concentric exercise
A, changes in MVC with exercise. Values have been expressed as the percentage of pre-exercise, which was assigned 100%. 0 h, values immediately post-exercise; 24 h, values 24 h later. Filled symbols, continuous line, values for exercised leg. Open symbols, dashed line, values for control leg. Dotted line indicates 100%. Asterisk indicates value significantly different from 'pre-exercise'. *B*, position errors at the knee. Filled symbols, continuous line, errors measured when the exercised leg acted as the reference leg. Open symbols, dashed line, the exercise leg acted as the indicator. Dotted line, zero error. Positive errors in the direction of leg extension, negative errors in the direction of flexion. All values are means (± S.E.M.). Asterisk indicates significant difference from pre-exercise errors.

Correlating position errors with fall in force

The data showed that both concentric and eccentric exercise led to position matching errors, and errors were larger when the fall in force was greater. This suggested that the force drop from exercise was correlated with the size of the errors. Because of the large amount of variability between trials and between subjects, individual values for force and position errors were poorly correlated ($r^2 = 0.06$). Therefore errors were pooled, regardless of their direction, both when the exercised leg acted as the reference and when it acted as the indicator. It meant that there were four points in the plot. Two values were for the eccentric exercise, immediately after the exercise (4.8 deg, 71.8%) and at 24 h (3.1 deg, 79.3%). Similarly there were two values for the concentric exercise: 3.7 deg, 84.6% and 2.1 deg, 98.8% for immediately after the exercise and at 24 h, respectively. A regression line was drawn through the data and it yielded an r^2 value of 0.82.

Discussion

The main result of this study was that after exercise of the quadriceps muscle it was possible to demonstrate a significant increase in position matching errors at the knee. The size of the errors was correlated with the fall in force (Fig. 5) suggesting that fatigue was a determining factor. After eccentric exercise the immediate fall in force was 30.2% and the error 4.5–6.5 deg (Fig. 3). After concentric exercise the fall in force was 14.5% and the error 2.1–3.0 deg (Fig. 4). These measurements are comparable to those made at the elbow joint (Allen *et al.* 2007). The errors were present after both eccentric and concentric exercise. Since no significant damage is evident after concentric exercise (Newham *et al.* 1983*a*, 1983*b*), it was unlikely that the errors were generated as a result of the muscle damage from the eccentric exercise (Proske & Morgan, 2001). This conclusion was supported by the finding that force had fully recovered by 24 h after the concentric exercise.

The way we have chosen to measure the effects of exercise on proprioception is by means of a position matching task. The experimenter moved one of the subject's legs to the reference angle and its perceived position was matched by voluntary placement by the subject of their other leg. We claim that this is a position matching task, although it could be argued that the subject is placing the indicator leg based on the remembered movement sensation accompanying placement of the reference leg. Such an interpretation would mean that the exercise effects would have to be interpreted in terms of a disturbance of movement sensation. The available evidence suggests that exercise does not disturb movement sensation (Allen & Proske, 2006).

After the reference leg had been placed by the experimenter, the subjects had to support it themselves. It could therefore be argued that this was not a position matching task but an effort matching task, the effort required to support the reference leg being matched during placement of the indicator leg. However, with such an interpretation the observed effects of the exercise are the opposite of what would be expected. It is known that fatigue from exercise impairs judgements of muscle force and that subjects are matching efforts rather than actual force levels (Gandevia & McCloskey, 1978; Jones & Hunter, 1983; Weerakkody *et al.* 2003). With such an interpretation the position of an exercised reference leg should have been matched by the subject placing their indicator leg in a more extended position, where the effort required to support it would be greater. The observed errors were in exactly the opposite direction.

After both forms of exercise, when the exercised leg acted as the reference, the errors lay in the direction of flexion. We placed particular significance on the fact that when the exercised leg acted as the indicator the errors were of a similar size but of opposite sign, that is, they now lay in the direction of extension. Such reversibility and symmetry of the errors made it unlikely that they could be attributed to factors other than the exercise, such as leg dominance or the way the matching task had been carried out. Errors always lay in a direction consistent with the interpretation that subjects believed their exercised quadriceps muscle to be longer that is actually was. Therefore when the exercised muscle acted as the reference, its position was matched by the indicator leg adopting a more flexed knee angle, representing a longer muscle. Similarly when the exercised muscle was the indicator, the leg adopted a more extended position, representing a shorter muscle.

At the start of the experiments we had considered two competing hypotheses. If the sense of effort accompanying support of the leg against the force of gravity was able to provide positional information, the extra effort required to support the leg with a fatigued quadriceps would have led the subject to believe that their leg was more extended that it was. An extended leg represents a short quadriceps, so this hypothesis predicts errors in the direction of extension when the exercised leg acted as the reference and in the direction of flexion when the exercised leg acted as the indicator. In fact, the observed errors were in exactly the opposite directions (Figs 3 and 4). The data supported the much simpler alternative hypothesis that an exercised muscle is always perceived as longer than it is.

Such a conclusion puts these observations in line with our previous reports (Walsh *et al.* 2004, 2006; Allen & Proske, 2006; Allen *et al.* 2007). The effort hypothesis had been based on the effects of exercise as well as on errors produced by loading the limb (Winter *et al.* 2005). The more recent observations on position matching at the elbow joint (Ansems *et al.* 2006; Allen *et al.* 2007) led to the realization that the errors and their direction in the experiments on loading the arm were influenced by how the reference and indicator arms had been

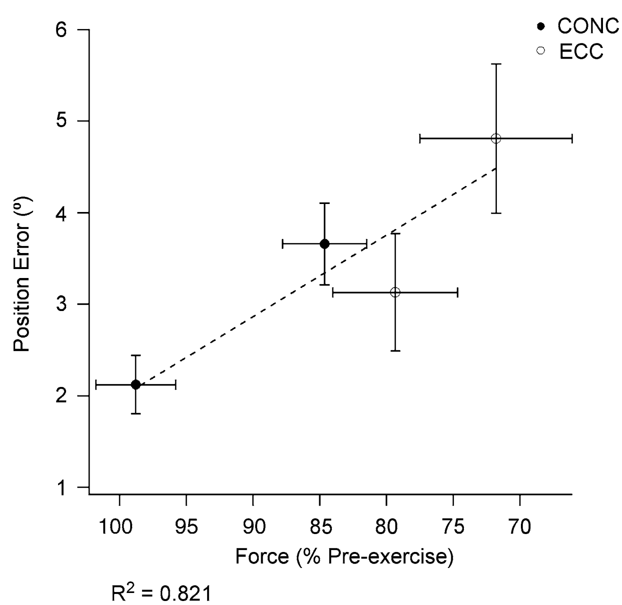

Figure 5. Error–force correlation
Plot of the relationship between matching errors for position sense at the knee and knee extensor force, expressed as a percentage of pre-exercise values. Position errors are differences between the exercised and unexercised leg and they have been pooled regardless of their direction. Filled symbols, data for concentric exercise measured immediately after the exercise and at 24 h; open symbols, data for eccentric exercise over the same time points. Values are shown as means (± S.E.M.). Dashed line, regression line ($r^2 = 0.82$).

conditioned beforehand. In this experiment quadriceps of both legs were always identically conditioned before each position matching trial so that conditioning effects were unlikely to play a role in the distribution of the errors. The fact that the position errors in this experiment were distributed in exactly the opposite direction to that predicted by the effort hypothesis goes against the idea of the sense of effort directly providing positional information.

Why might an exercised muscle be perceived as being longer that it is? We have previously interpreted the effects of loading of the arm and of exercising it on the operation of an internal forward model (Wolpert *et al.* 1995; Bays & Wolpert, 2007). In such a model, feedback from the motor command accesses past memories of such movements, leading to a comparison between anticipated and observed feedback. When feedback delays prevent an immediate comparison, the predicted signal operates on its own (Dassonville, 1995; Wolpert *et al.* 1995). The outcome of the comparison leads to perception of only the difference between them. When the limb is loaded, the predicted and fed-back signals coincide since such conditions have arisen in the past. This is not likely to be so for the effects of exercise. Previous experience of position sense with a non-fatigued muscle might provide a prediction for sensory feedback that was less than what actually occurs during support of the limb with a fatigued muscle. The larger than expected feedback would be perceived as a longer muscle, consistent with the direction of the observed errors (Allen *et al.* 2007). It now remains to obtain more direct evidence in support of such an interpretation.

Apart from the insight it provides into mechanism, does the effect of exercise on proprioception have any additional relevance? Clearly, during skilled sporting activities erroneous proprioceptive signals as a result of fatigue risk deterioration in performance, in addition to any effects from the loss of muscle force.

In an epidemiological study of the risk factors associated with falls in elderly subjects, one of the factors identified was poor proprioception (Lord & Ward, 1994). Therefore any activity that further disturbs proprioceptive acuity would increase the risk of falls. Unaccustomed exercise in untrained elderly subjects would be expected to be initially accompanied by an increased risk of falls. It would be interesting to put such a prediction to the test.

To conclude, these experiments have demonstrated that after exercise of the quadriceps muscle, position matching ability is disturbed, with subjects perceiving their exercised muscle to be longer than it is, leading to matching errors. Such disturbances can be interpreted by operation of an internal forward model. The errors in proprioception may be a contributing factor to injury from fatigue in sport or exercise.

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